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NOTES ON THE RELATIONSHIP BETWEEN THE FRESH-WATER MUSSEL *ANODONTA IMPLICATA* SAY AND THE ALEWIFE *POMOLOBUS PSEUDOHARENGUS* (WILSON)[1]

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"Were there more connections between us that needed exploration?"—John Hay: The Run.

ABSTRACT

An ecological relationship between the freshwater mussel *Anodonta implicata* Say and the alewife *Pomolobus pseudoharengus* (Wilson) is described. Evidence is presented that the parasitic larvae (glochidia) of *A. implicata* cannot, in the process of attachment, "discriminate" between the tissues of *P. pseudoharengus* and those of other fishes that may move with the alewives during the run but have a much wider distribution. The conclusion is reached that if, as most evidence appears to indicate, the relationship between the two animals is nevertheless a species-specific one, the parasitic stage of *A. implicata* cannot complete its development on the tissues of other fishes to which it can be caused to attach experimentally and, further, that this stage can be of no greater duration than the time spent in freshwater by an individual alewife.

INTRODUCTION

Baer (1952, p. 22), in discussing the parasitic larval stages of freshwater mussels, says that "... experimentally glochidia may be made to attach themselves to many kinds of fishes and even to tadpoles and axolotls, yet it appears that complete larval development can be obtained only when glochidia affix themselves to particular species of fish which seem to be fairly specific for a given mussel." However, a *strict* species-specificity in which the parasite is limited to one host only, appears to be the exception rather than the rule among such glochidial-fish relationships. Surber (1912) lists the sheepshead, *Aplodonotus grunniens*, as being the sole host of the paper shell *Lampsilis laevissima* and of the deer toe *L. donaciformis*; the shovel-nose sturgeon, *Scaphirhynchus platorhynchus* as the host of the slough sand shell, *L. fallaciosa*; and the skipjack of the Mississippi drainage, *Pomolobus chrysochloris*, as the host of *Fusonaia ebena*. The specificity of the last relationship is of particular interest to us, in view of the close systematic position of *P. chrysochloris*, the skipjack and *P. pseudoharengus*, the alewife. One might well ask if there is something about the genus *Pomolobus* that is conducive to the formation of species-specific relationships with certain glochidia.

Johnson (1946) published a short paper clarifying the taxonomic status of the mussel *Anodonta implicata* Say and establishing types for the species. He says (p. 113) "So far as is known it ranges from New Brunswick and Nova Scotia south to Virginia, being restricted to ponds and streams near the coast that are frequented by the alewife . . . ." and (p. 112) ". . . the

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[1] The authors present this work in the hope that it will bring to the attention of limnologists a complicated and fascinating problem of more than local interest and in the belief that, although only a small contribution, it serves well to honor a man who has given much of his life with love to the natural history of the Cape Cod area.

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glochidia of *A. implicata* have been found by the author on the gills of the host as well as the fins." He lists many records for this mussel and presents a map of its distribution that is surely indicative of a distribution paralleling that of an anadromous fish. There is excellent evidence that the mussel has disappeared from lakes in which it was once common before the runs of anadromous fishes were cut off by pollution or dams, such as Fresh Pond, Cambridge, Massachusetts (R. Johnson and W. J. Clench, personal communications). To date, there are no records of the glochidia of *A. implicata* appearing on the appendages of fishes other than the alewife.

Whenever a case of strict species-specificity of this type appears to be at hand, one suspects that there may be some information exchange between the two species and that the parasite may be competent to show some "discrimination" in host selection. It has been established for some time that glochidia do not appear to be able to give a *directional* response to their host. They do not actively "search for and find" their hosts, yet it cannot be assumed that they may not give a "selective" contact-chemical response when encountering host tissues.

The questions arose as to a) whether the presence of the alewife is necessary for the release of the glochidia of *A. implicata*, and b) whether the gochidium of *A. implicata*, recorded only from the alewife, "recognizes" its host and attaches to it by preference when experimentally given an opportunity to select a host from among other species of fishes in the same environment.

MATERIAL AND METHODS

Live alewives were collected periodically (7 May 1965 and thereafter) at the narrows between the two Mystic Lakes, Middlesex County, Massachusetts. These were maintained successfully for a number of days before sacrifice for experiment in large shallow aquaria provided with tap water. *A. implicata* were collected during the spring months (March to May) from the Agawam River, approximately 2 miles (3.2 km) south of Half-Way Pond, Plymouth County. These animals were found in large numbers (50–100 in an area 4.5 m square) in the sandy bottom of the river over which large numbers of alewives migrate annually. On being transported back to the laboratory, they were maintained successfully for several weeks in water-tables supplied with tap water. Many individuals had their marsupia so heavily loaded with ripe glochidia in the early spring months that a single individual could provide enough larvae for many experiments; this species of mussel has proved to be an ideal donor of experimental glochidial material. In addition, the first of the questions posed above was answered when it was found possible to induce release of countless glochidia merely by allowing the animals to reach room temperature; the majority of mussels so treated released clouds of glochidia into their aquaria within 48 hr after the temperature had reached 20C. Furthermore, glochidia could be obtained at will from gravid mussels by killing the mussels and excising the marsupia; under these conditions the glochidia behaved in a completely normal way and exhibited immediate "winking" activity upon being released in water.

The three nonhost fish species used in the experiments to be described were obtained directly from an alewife ladder in the Agawam River; along with alewives in the ladder, they had passed directly over large beds of *A. implicata* in their movements to the ladder from downstream. Movements of suckers, sunfish, and other fish, along with the alewife runs are described by Hay (1965); they appear to be an integral though limited part of the total moving population, preying upon the eggs laid by the alewives.

A test apparatus consisted of a plastic disk, with plastic fins on its lower surface which served to keep water moving. When the disk was slowly rotated on an electric stirrer, in a plane parallel to the bottom of a circular glass aquarium, continuous currents were produced. The disk had four equidistant holes drilled at 90° angles to each other on the margin. To these holes one could attach four small fishhooks on fine nylon leader material. The test tissues to be presented to glochidia, could be attached to the hooks and the disk lowered to a point where all preparations could be dragged over the bottom at approximately the same level, giving glochidia that had settled on the bottom or were moving in the currents of the aquarium a relatively equal opportunity to attach themselves to preparations placed on the test apparatus. In a standard test, an opposite pair of hooks (controls) held an alewife pectoral fin and a pelvic fin, while the other pair of hooks at 90° from the former held pectoral and pelvic fins of species to be tested.

When a test was to be conducted, the marsupia of a gravid *A. implicata* were excised and a larger number of glochidia (many hundreds) teased out into water in a finger bowl. These were checked for activity and if normal were set aside for use when the fish preparations had been made. Next, a live alewife was removed from the aquarium, killed, and the pelvic and pectoral fins were excised and immediately hung on two opposite hooks. Nonhost fins were similarly freshly prepared from newly killed animals, attached to the remaining two opposing hooks, and the whole apparatus was then lowered into the test aquarium so that much of the surface of each fin lay gently on the bottom. The stirrer was then started and the fresh, active glochidia poured into the system when it had reached constant velocity. Such a test was allowed to continue overnight (12–15 hr). At the end of a test, all fins were removed, each one was vigorously shaken in clean water so as to remove any glochidia that were lightly adhering to surfaces, and checked for firmly attached, *closed*, glochidia.

EXPERIMENTS AND RESULTS

Experiment Number 1. Two alewives caught at the beginning of the Falmouth run in the early spring were frozen overnight in a freezing compartment. On the next day, fins of these fish were excised, thawed, and suspended in an aerated and stirred aquarium into which several hundred active glochidia had been introduced. At the end of 12–15 hr, no attachment whatever had occurred.

Experiment Number 2. A live alewife maintained in the laboratory was killed, the pectoral and pelvic fins were immediately excised and suspended with active glochidia in the test apparatus described above. At the end of 12–15 hr, large numbers of glochidia had become firmly attached to the edges of the fins and the soft tissues between the rays.

Experiment Number 3. Three consecutive tests were run with opposed freshly excised pectoral and pelvic fins: *P. pseudoharengus* vs. the white sucker, *Catostomus commersonii*; *P. pseudoharengus* vs. the pumpkinseed sunfish, *Lepomis gibbosus*; and *P. pseudoharengus* vs. the white perch, *Morone americana*. In none of these tests, in which the fins of three species occurring directly in the alewife run were presented, did the glochidia give evidence of any discriminatory activity. They attached themselves in large numbers by closing firmly on the margins and soft tissues in between the rays of the fins of all four species.

Our technique did not lend itself to a precise comparison of numbers, because size differences in the fins affected currents and the consequent concentrations of "settled out" glochidia; the chances of attachment were not precisely equal. Subjectively, attachment seemed slightly more effective on alewife fins, but to be sure of this many such experiments would have to be conducted with careful counts of attached glochidia per unit area being made under precisely similar opportunity of attachment.

DISCUSSION

The first of the questions posed above was answered by the laboratory observations on the effects of temperature increases in triggering the release of glochidia. It is clear that the presence of the alewife is not necessary for glochidial release to occur. Whether some sign from the alewife schools facilitates glochidial release remains to be investigated. Similarly, the relationship of temperature and time in triggering the release of glochidia should be determined under natural conditions.

The experiments gave evidence that although glochidia may require that certain chemical or physical characteristics be maintained in a tissue for attachment to occur, they do not, under the experimental conditions employed here, appear to show any significant discrimination in host attachment.

It is clear that for a thorough clarification of the relationship of *P. pseudoharengus* and *A. implicata*, detailed field and laboratory studies will be required. Possibly the relationship is not a specific one and the mussel may carry out its development on other anadromous fishes with a range similar to that of the alewife, such as the white perch. One would like to know whether, under experimental conditions, the mussel could be made to pass through the parasitic part of its life cycle on species closely related to the alewife, such as the glut herring, *P. aestivalis* (which occurs in the lower part of the same drainages) or the shad, *Alosa sapidissima.* Failure to show attachment specificity is, of course, no evidence that the glochidia can complete their development on other species; as in many other Unionidae, these glochidia may be prevented from so developing as a result of failure to effect implantation or cyst formation because of some physiological characteristic or immunological mechanism.

However, if it is assumed, as most of the evidence indicates, that the alewife is the specific host of *A. implicata*, one can make some generalizations about the distribution of the latter based on knowledge of the habits of both species. Our own field observations support those of Johnson (1946) in that we have found *A. implicata* to be far more successful in streams than in ponds. The extremely high concentrations in the sandy bed of the Agawam River directly under the course of the alewives is mentioned above. The mussels are common enough in absolute numbers in ponds where alewives spawn, but they are far less concentrated than in the outlets; a transect along the upper end of Great Herring Pond at the head of the Bournedale run produced a mussel about every 3–5 m. In our experience, the animals present in streams (Agawam River, Bourne Run, and so on) are larger and handsomer than pond specimens; clearly the former are in the optimal environment. Aside from any physiological adaptation to development on alewives alone, the ecological factors that produce such a distribution are fairly clear. It is known that the alewife run is triggered by a rise in temperature (Massachusetts Division of Marine Fisheries 1963), and apparently the release of glochidia by the mussel is also so triggered. Even in the face of the possibility of the completion of development on other species, the vast preponderance in numbers of alewives during the spring and summer months over other species makes them the most effective dispersal agent, and a temperature-timed mechanism that would cause the release of glochidia in the midst of an alewife run would produce an infection that would insure distribution of the mussel over the extent of that run. If the laboratory observations of glochidial release are any indication of what happens in nature, the mathematical probabilities of any appreciable proportion of alewives in a horde moving over a mussel bed avoiding infection by glochidia from the "shotgun blasts" emitting from the excurrent siphons would be low indeed, particularly in the narrow waters of a stream bed.

One interesting point remains. The attached existence of the glochidial stages of Unionids is known to be fairly short; according to Lefevre and Curtis (1910), Harms found the duration of the parasitic stage of a European *Anodonta* to be only 21 days at 18C. This is quite short enough to allow completion of the parasitic stage of *A. implicata* in time for the developing mussel to be dropped off at the end of the stay of the alewives in their breeding ponds or on the run downstream. Indeed, unless young mussels are carried down out of the ponds by spring freshets or unless they are far more active than one would suspect, they must be dropped in their optimal environment—the stream—by a precise developmental timing correlated with the time of return of the alewives. Current studies in the Department of Fishes of the Museum of Comparative Zoology indicate that only a small fraction of an alewife run represents second-time "runners." It seems extremely unlikely that the glochidial cysts could pass a winter at sea on the fins of an alewife, and even if they did their chance of return would be small.

The above conjectures and conclusions are primarily designed to bring the attention of ecologists to the possibilities for the investigation of a relationship involving two readily controllable and measurable animal populations. This should be carried out in the optimal environment where th mussels, alewives, and associated fishes ca best be obtained and maintained—the clear sand-bottomed streams that empty th ponds of the Cape Cod area.

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